

CHAPTER 12

ECOSYSTEM-LEVEL FACTORS THAT MAY AFFECT RESTORATION OF SEABIRD POPULATIONS

INTRODUCTION

Some marine bird populations have been reduced by specific and persistent factors: the introduction of pesticides into the food web (e.g., DDT and the brown pelican, Anderson and Gress 1983); oil pollution (e.g., common eiders in the Rhine River, Camphuysen 1989; common murre on the Farallon Islands, Ainley and Lewis 1974); hunting (e.g., thick-billed murre in the eastern North Atlantic, Gaston and Elliot 1991); or the introduction of mammalian predators to breeding islands (e.g., rats, cats, mongooses, and humans and the dark-rumped petrel on Hawaii, Olson and James 1982, Harrison 1990). Other populations have been reduced by more systemic factors, such as curtailment of prey availability (e.g., the Peruvian guano birds, Murphy 1981, Tovar *et al.* 1987a).

The question is, can depleted seabird populations be guided back to their former state?

We argue herein that establishing restoration goals relative to a baseline defined by historical, or even the immediate, pre-impact population size is, at best, an illusory concept in marine systems. Because seabirds are positioned high on the trophic pyramid, they integrate and are sensitive to the ecological and food-web processes in the systems "beneath" them (e.g., Furness *et al.* 1993). Unfortunately for the purposes of restoration, marine systems are characterized by marked decadal variation (e.g., Longhurst *et al.* 1972, McGowan 1990), and may be too big or affected too greatly by large-scale physical processes (e.g., Sherman and Alexander 1985, Sherman *et al.* 1990, 1993) for humans to guide specific restorative processes toward a predictable goal. Thus, factors at play in the larger system most likely will dilute any isolated, local factors that may have affected trends in a seabird colony or population.

GENERAL CONSIDERATIONS

Factors That Limit Population Size: Is Competition Involved?

The size of breeding populations of seabirds is thought to be controlled by either space for nesting, the amount of prey available to foraging parents, or the amount of prey available to the population during the time of year when food is least abundant or accessible, usually the winter (Lack 1966, Furness and Birkhead 1984, Cairns 1992). These factors are further discussed below

Limitation by nesting space

In highly productive areas where there are few nesting islands, such as eastern boundary currents, the availability of nesting space is clearly the factor limiting the size of breeding numbers (but see Chapter 3b for different view). Such seabird communities are structured by competition for nesting habitat (Duffy 1983, Duffy *et al.* 1984, Ainley and Boekelheide 1990). In these situations, "floating populations" develop and are composed of birds that are capable of breeding but that lack breeding space (Manuwal 1974b, Ainley and Boekelheide 1990, Migot 1992). Any growth in numbers is limited to this nonbreeding portion of the population; the breeding population remains stable, being constantly sustained by the pool of waiting nonbreeders. Ultimately, the size of the total population (breeders and nonbreeders) may be limited by food or by a series of catastrophic mortalities resulting from periodic food shortage (e.g., mediated by repeated El Niños; Nelson 1968, Schreiber and Schreiber 1989).

Where nesting space is limited, breeding populations increase only by the provision of new nesting sites. In the Benguela Current, vast nesting platforms were constructed to increase the numbers of guano-producing Cape cormorants and Cape gannets, and provision of artificial burrows has increased numbers of breeding African penguins (Crawford and Shelton 1978, Crawford *et al.* 1995). In the Peru Current, natural predators were eliminated or excluded by fencing to open new nesting areas. After these areas were colonized, there was a manyfold increase in the numbers of guano-producing seabirds—Peruvian pelican, piquero and guanay (Duffy *et al.* 1984). In the California Current, artificial nesting cavities were used readily by several species of seabirds—especially pigeon guillemot and Cassin's auklet—during a period of population expansion (Ainley and Boekelheide 1990). More recently, as the carrying capacity of that environment has decreased (Hill 1995, Roemmich and McGowan 1995; see below), the use of artificial nesting habitat has also decreased (Point Reyes Bird Observatory [PRBO], unpubl. data). Another example exists in Prince William Sound, where a glacier receded in the 1960s, exposing a rocky island; by 1985 more than 5,000 seabirds were nesting there (Hogan and Irons 1988).

Limitation by food during breeding

Where breeding sites are numerous but food is not especially abundant, such as in the waters around the British Isles, the size of breeding populations is controlled by the amount of food available to parents feeding for chicks (Furness and Birkhead 1984, Cairns 1992). These seabird communities appear to be structured by the competition for food. The mechanism by which this structuring could come about is the reduction in reproductive capacity owing to the local depletion of prey (e.g., Birt *et al.* 1987) or interference competition (Gaston *et al.* 1983, Hunt *et al.* 1986). In a "natural experiment" in the North Sea, seabird populations declined as stocks of their usual prey (sandeels) declined, possibly related to the heavy commercial fishing pressure (Furness 1982, 1984a, 1984b, 1989; Hammer *et al.* 1991, Phillips *et al.* 1996).

The availability of food to foraging parents may also limit the size of breeding populations of tropical, oceanic species (Ashmole 1963). There, and in other situations, the size of a breeding population of a given species relative to population size of others in the breeding assemblage is

in proportion to the area of foraging habitat available: species feeding inshore have small populations compared to the large populations of species feeding in the practically limitless offshore habitats (Diamond 1978). The major limit to the amount of ocean area available is the flight range of nesting birds (e.g., Pennycuick *et al.* 1984) and the capacity of chicks to forgo frequent feedings.

In polar regions, where food is very abundant for a short period and where nesting space seems unlimited as well, the physical severity of the climate may be an overriding factor in population regulation. At the least, the severe climate often masks the ultimate regulatory factors because, owing to birds' need to escape from particularly inclement weather, breeding areas are greatly separated from wintering areas. For example, a lessening of pack-ice cover—in a sense an indirect change in the accessibility of food—may have mediated changes in populations of nesting penguins and other species in the normally icebound areas of Antarctica (Ainley and Sanders 1989, Taylor and Wilson 1990, Fraser *et al.* 1992). On the other hand, a change in food supply thousands of kilometers away on the ice-free wintering grounds may have mediated changes in breeding population size among murres in the northeastern Bering Sea (Murphy *et al.* 1985).

Limitation by food during winter

Seabird populations may also be regulated by food in the season when it is least abundant, which is usually the nonbreeding season, or winter (Lack 1966). Direct evidence for this is sparse because, as indicated in the above paragraph for murres in the Bering Sea, wintering grounds of seabirds are often far away from breeding sites. Nevertheless, during winter (1) numerous "wrecks" or mass mortalities of seabirds have been documented (e.g., Richdale 1957, Bailey and Davenport 1972, Birkhead and Hudson 1977, Piatt and van Pelt 1993); (2) the most difficult time for immatures occurs (e.g., Harris 1983, and virtually any long-term demographic study); and (3) elevated levels of adult mortality are detected (e.g., penguins, Richdale 1957; gulls, Bergman 1982, Spear *et al.* 1987; alcids, Hudson 1985).

Vader *et al.* (1990) documented a sudden decline of common murres at colonies in northern Norway in 1987, and attributed this decline to a food shortage resulting from a collapse of capelin stocks in the Barents Sea. They hypothesized that either the breeding population of common murres died from starvation during the winter of 1986-87, or that adults were unable to build up enough energy during the winter and spring, and abandoned all breeding attempts. An unusual late winter wreck of shags in eastern Britain was caused by a prolonged period of onshore winds, possibly resulting in a food shortage (Harris and Wanless 1996). This wreck was composed equally of adults and immatures, and affected all colonies along at least a 100-kilometer stretch of the coast. Harris and Wanless (1996) reported that this wreck was unprecedented in the number of adult birds killed, causing a reduction in annual survival rates from a normal 88% to 13%; the Isle of May shag population may require 10 years to recover from the decline.

The role of competition

Ultimately then, competition, as a result of resource limitation, could well affect the size of a population. However, in a depleted population—a candidate being considered for restoration—*intraspecific* competition should not be a problem (although under stable conditions, competition should be most intense within a species; Birkhead and Furness 1985). *Interspecific* competition for food among seabird species has rarely been demonstrated, except possibly interference competition on the part of sooty shearwaters and other species (Hoffman *et al.* 1981), interference competition between lesser black-backed gulls and herring gulls (Noordhuis and Spaans 1992), and shifts in foraging behavior of ducks (Pöysä 1986). Interspecific competition for food between seabirds and other organisms, such as whales (in the southern oceans, Beddington and May 1982, and the Bering Sea, Springer and Roseman 1985), may be another matter, but in recent decades whales have been depleted and, therefore, should have no negative effect on seabird food availability. Seabirds may also compete with upper-trophic-level predatory fish in certain systems, (e.g., the Bering Sea, Springer 1992, or the North Sea, Furness 1984a). When the exploited fish is a competitor, its reduction in prevalence increases the availability of prey to seabirds (e.g., Bering Sea auklets that feed on the zooplankton eaten by pollock). Conversely, when the exploited fish are seabird prey, the seabirds are negatively affected (e.g., Bering Sea murrelets that feed on juvenile pollock; Springer 1992).

In the case of nesting space, competition among cavity-nesting seabirds has been mediated through body size (e.g., Bédard 1969a, Ainley and Boekelheide 1990), but seabird species tend to nest where others are already nesting, with little evidence for outright exclusion (e.g., Whittam and Siegel-Causey 1981). On the Farallon Islands, as common murre and Brandt's cormorant populations recovered during the 1970s, the high density of murre nesting groups allowed them to move the larger cormorants, but the cormorants then displaced western gulls, who did not nest densely enough to cope with the cormorants' greater body size (Ainley and Boekelheide 1990). In the northwestern Hawaiian Islands, if chicks of the smaller, winter-breeding Bonin petrel remain late, they are displaced by the larger wedge-tailed shearwaters when the latter return to initiate breeding in the same cavities (Harrison 1990). In the Azores, the smaller little shearwater breeds during the winter, possibly to avoid competition for nesting space with the larger Cory's shearwater, which nests during the summer. For the same reasons, morphologically distinct forms of the band-rumped storm-petrel breed in the summer and fall (Monteiro *et al.* 1996), and morphologically and taxonomically distinct forms of the Leach's storm-petrel breed in opposite seasons on Guadalupe Island (Ainley 1980).

One other aspect of the competition for food and space concerns the concept of source versus sink populations (see Chapter 3). Where there is plenty of food but limited nesting space, colonies become source populations because the easiest avenue by which individuals can recruit into the breeding population requires emigration elsewhere. On the other hand, where limited food or too much predation exists but there is plenty of space, such colonies may become sinks. Individuals recruit to them, but breeding success is low and the colony cannot be sustained without immigration from source populations. The latter is the case among South Polar skuas at Cape Crozier (Ainley *et al.* 1990). The colony there is the largest for this species in the world,

but it is sustained by immigrants attracted to plentiful food. Breeding success, however, is almost nil at Crozier, owing to intense storms that blow away eggs and chicks.

In addition to structuring nesting dispersion on the temporal scale, competition can also structure the spatial dispersion of nesting. Around the British Isles (Furness and Birkhead 1984) and in Antarctica (Ainley *et al.* 1995a), competition for food has been identified as a factor that prohibits large colonies of certain species from occurring in proximity to one another. Instead, only small colonies, often in a cluster around the larger colony, can exist nearby. Emigrants from the large (source) colony initially colonize these peripheral localities, and the entire cluster of colonies must be viewed as the "population" (or metapopulation; see Chapter 3).

Whether a colony is a source or a sink—or, for that matter, whether a population is food or space limited—is not necessarily static. Over an extended period, colonies may switch from being a source to a sink or vice versa. For instance, the sudden availability of nesting space (retreat of a glacier, construction of a dredged materials island, etc.), which is then colonized, leads to a sink initially. If the site is especially favorable (e.g., good feeding opportunities, free of predators, free from disease, etc.), it could grow to become a source colony within a few generations. For instance, not long ago in northern Europe and in North America the herring gull was food limited, but with the growth of human refuse dumps and the increased availability of fishing offal, the population has become space limited (e.g., Migot 1992). As other examples, populations of ring-billed gulls in the Great Lakes region and guano birds in Peru grew in response to increased food until they became so dense that disease (botulism and parasites, respectively) began to increase mortality (Blokpoel and Scharf 1990, Duffy 1991).

FACTORS THAT LIMIT OR ENHANCE RECOVERY

Temporal and Spatial Scale of Perturbation

Scale has much to do with the relationship of populations to their resources (Schneider 1994). Where short-term, localized mortality has affected a satellite colony in a larger metapopulation, colonies often recover their former size in a few years, owing to adequate resources more widely distributed than the perturbation and to recruits from the source colony. A classic example is provided by European shags on Farne Island. In 1968, they experienced a red tide and the population crashed from 350 to 75 pairs (Potts *et al.* 1980). However, within six years, the numbers recovered completely as a result of both immigration from nearby colonies (not affected by red tide) and recruitment of individuals who were otherwise not breeding due to a prior lack of breeding space.

Another example is that of the Peruvian guano birds. Before the 1970s, there was a large "floating" population composed of individuals precluded from breeding by lack of a breeding site in spite of periodic large-scale mortality due to lack of food (caused by El Niño). Once the food web was re-established, *breeding* populations recovered too quickly to be the result of renewed breeding success (Murphy 1936, Tovar *et al.* 1987a; although D. Duffy, pers. com., indicates that recovery might be the result of high productivity and not a large "floating"

nonbreeding segment of the population). A third example is offered by Stowe (1982), who noted a decrease in numbers of murres at colonies immediately following an oil spill nearby. Within a year, however, the colonies returned to or even exceeded prespill numbers. The adults who had not been breeding, plus recruits from juveniles who had recently matured, accounted for the increase. The same can be said of rapid recovery from a short-term mortality experienced by rhinoceros auklets on the Farallon Islands.

Conversely, where there is long-term, pervasive mortality that affects all generations of a metapopulation, recovery requires decades to complete. For example, the Farne Islands shag population, following release from a long period of persecution, grew for 45 years beginning with a decade of virtually no growth. Another example is offered by king penguins on Macquarie Island. They had been hunted to the point of near-extinction, and recovery took about 80 years (Rounsevell and Copson 1982). In the first 20 years following the cessation of hunting, the population showed no growth. This pattern was due to the fact that Macquarie Island is very isolated, and little if any immigration was possible from other colonies or metapopulations. Therefore, all growth had to be intrinsic. In the case of the slow-maturing wandering albatross (it first breeds at 12 years of age), which has been declining at many disjunct breeding colonies for several decades owing to mortality of females from entanglement in fishing gear (Weimerskirch and Jouventin 1987, Croxall *et al.* 1990), prospects for a fast recovery are similarly low should the fishing mortality be curtailed. Finally, a population can persist in a depleted state due to the cumulative effects of impacts that occur one after another, as is the case of murres on the Farallon Islands. In the late 1800s, uncontrolled commercial eggging reduced the population from an estimated 400,000 birds to 40,000, followed by several decades of oil pollution and other disturbance, which reduced the population still further, to 6,000, by the 1960s. Control of impacts allowed the population to grow to almost 100,000 by the early 1980s, but gillnetting and oil spills then reduced the population again to 40,000 birds (Ainley and Lewis 1974, Ainley and Boekelheide 1990). A similar example is offered by penguins in southern Africa. First diminished by disturbance (mining of guano) and exploitation for eggs, penguin populations, upon protection from these impacts, were reduced still further by a series of oil spills and finally overfishing of their prey by commercial fisheries (Crawford *et al.* 1995).

Food Availability

The population dynamics of seabirds track food availability more than any other ecological factor (Furness and Monaghan 1987, Cairns 1987, Montevecchi 1993, and others). For example, when predatory fish were heavily fished in the North Sea, their prey (sand lance) bloomed and seabird numbers increased, but when numbers of sand lance crashed at Shetland, so too did the reproductive success of many seabirds and in some cases their population size (Furness 1982, 1984a, 1989; Monaghan *et al.* 1989a, 1989b; Hamer *et al.* 1991, Phillips *et al.* 1996). Decline in North Sea herring stocks was associated with a decline in kittiwake reproductive success (chicks fledged per pair) and a decline in population growth rate (Coulson and Thomas 1985). A similar seesawing of prey availability as a function of fishery pressure is perhaps also being played out in the Bering Sea with respect to pollock. Seabirds that feed on small pollock are declining (e.g.,

murres), but those that feed on the zooplankton prey of pollock are increasing (e.g., auklets; Springer *et al.* 1986, Springer 1992).

The Peruvian guano birds represent another and perhaps better example: overfishing of anchoveta, the mainstay in the diet of many predators, in conjunction with environmental stress, caused a crash in the fish stocks and, in turn, a dramatic decline in numbers of boobies and cormorants and in the ability of these seabirds to recover from periodic El Niños (Tovar *et al.* 1987a). El Niño in 1957 (and earlier episodes) caused crashes in guano bird populations, followed shortly by full recovery. Then, beginning with the onset of overfishing of the anchoveta, following each subsequent El Niño (1965, 1972) each seabird population recovery was weaker than the preceding one—that is, the carrying capacity of the environment began to change.

Other examples of how food availability influences recovery are provided by common murres. On the Farallon Islands, the murre population partially recovered during the 1970s and 1980s, having been released from the effects of disturbance and chronic oil pollution, as noted above (Ainley and Lewis 1974, Ainley and Boekelheide 1990). Between 1982 and 1986, however, the murres in the entire central California metapopulation were subjected to heavy mortality from gillnets, a severe El Niño, and two oil spills (Takekawa *et al.* 1990). As a result, the populations of all colonies crashed. Although these perturbations did not extend beyond 1986, none of the colonies in the metapopulation have shown substantial recovery since, in spite of high breeding success (Ainley *et al.* 1994). Coincidentally, many of the murres' prey species are being fished intensively, with fishing pressure increasing dramatically during the 1970s and 1980s (Ainley *et al.* 1994). Lack of recruitment in the fish populations owing to changed oceanographic conditions, too, is likely involved (see below).

The lessening of carrying capacity may also explain why the Farallon murre populations in the 20th century have never come close to recovering their mid-19th-century size, which was 400,000 birds (cf. Ainley and Lewis 1974, Takekawa *et al.* 1990, Ainley *et al.* 1994). As pointed out by Roemmich and McGowan (1995), major changes in the California Current after the mid-1970s resulted in a dramatic reduction in zooplankton biomass. At the same time, fisheries were growing dramatically (Ainley *et al.* 1994). As a result, the trophic environment is different now compared to that of former years. Not only breeding species, but nonbreeders such as the sooty shearwater, have demonstrated depressed populations in response to the poorer feeding conditions (Ainley *et al.* 1995c, Veit *et al.* 1997). Similarly, the "recovery" of the brown pelican in California is stalled—that is, it is stable and self-perpetuating but below the level reached during pre-DDT years (reviewed in Ainley and Hunt 1990). If sustained, a resurgence of the sardine in California (Barnes *et al.* 1992, Wolf 1992), formerly the primary prey of pelicans in California (MacCall 1984), may encourage a period of renewed growth in the pelican population.

The recovery potential of a seabird community can also be affected by changes in the quality, or species composition, of the prey base. The classic example is provided by seabirds in southern Africa (Crawford and Shelton 1978). There, fisheries caused regional shifts in the distribution of various fish species and, in turn, the breeding distributions of some seabird species. The same type of shift has been documented in Peru and Chile beginning in the 1970s. To some degree,

the depleted anchoveta were replaced by sardines, but only in an area poleward of the previous anchoveta concentration (Bakun and Parrish 1982, Parrish *et al.* 1982). Seabird populations shifted southward too, although not in the same numerical mix of species that occurred to the north (Tovar *et al.* 1987b). This shift southward repeated the same pattern that occurred between the 16th and 19th centuries (Hutchinson 1950). Similarly, the northward shift of northern gannets in Newfoundland was correlated with a warming of the Labrador Current (and a northward shift as well in mackerel, the birds' main prey; Kirkham and Montevecchi 1982).

Influence of Disturbance on the Breeding Effort

Unnatural disturbance can also negatively affect the recovery potential of seabird breeding colonies. Often, an effective management practice promoting recovery of seabirds, and perhaps one of the few practically available, is protection of breeding colonies from eggging, hunting, and disturbance. Scores of species have benefited from protection, including king penguins on Macquarie Island (Rounsevell and Copson 1982), Laysan albatross on Midway Island (Rice and Kenyon 1962), northern gannets in Newfoundland (Brown and Nettleship 1984), cormorants in eastern North America (Buckley and Buckley 1984), common murres on the Farallon Islands (Ainley and Boekelheide 1990), and Atlantic puffins in Europe (Harris and Wanless 1991).

The disturbance does not have to be direct, as indicated by cases in which breeding colonies are abandoned owing to the threat of predation by mammals. Even if few or no eggs, chicks, or adults are taken, adults refuse to begin their breeding efforts once a mammalian intruder is spotted. An example is abandonment of nesting islands in Mono Lake, California, by California gulls when landbridges allowed the entry of coyotes onto the breeding islands (Winkler and Shuford 1988; W. Shuford, pers. com.). Another example is abandonment by murres when weasels and foxes make their way over sea ice to offshore islands in Newfoundland (Birkhead 1993, Birkhead and Nettleship 1995). Finally, growing populations of pinnipeds, if present on islands during the seabird breeding season, can disrupt the breeding efforts of the birds (Shaughnessy 1984, Warheit *et al.* 1984, Warheit and Lindberg 1988, Ainley and Boekelheide 1990). Recently in southern Africa, pinnipeds have been fenced from the breeding areas of African penguins to allow recovery of penguin populations depleted by oil spills (Crawford *et al.* 1995).

The response of seabirds to disturbance and their recovery once disturbance is controlled is not always a simple matter. For instance, the number of Adélie penguins at the small colony at Cape Royds, Antarctica, decreased during the period 1956-63, ostensibly due to too-frequent visits by tourists (Thomson 1977). When human visitation was reduced, the penguin population began to increase by 3-4% through 1973. Interestingly, the period of decline at Cape Royds coincided with a decline of Adélie penguin numbers at the region's major (source?) colony, Cape Crozier, where tourist visits were not occurring (cf. Ainley *et al.* 1983, Taylor *et al.* 1990). In more recent years, the rate of increase at Cape Royds has grown to 5% per year, an adjacent colony has been re-established after a hiatus of over 80 years, and all colonies in the region have been increasing, including the one at Cape Crozier (Taylor and Wilson 1990). More penguins now breed at Cape Royds than in any other time in recorded history. In retrospect, it is now obvious

that the period of decline at Cape Royds coincided not only with uncontrolled disturbance from human visitation but also with a period of cold weather and more dense pack-ice on the sea (thus increasing the energy cost of reproduction by limiting access to open water). The population increase was aided by a period of warming during which time the source colony of the metapopulation was also expanding rapidly (Taylor and Wilson 1990).

Effects of Predators and Kleptoparasitism on Population Growth

Interactions among seabird species, specifically the predation of small species by large ones (e.g., gulls, skuas) or the kleptoparasitism of food by large species (gulls, skuas, frigatebirds) against smaller ones, have led to adaptations in life history patterns. For instance, a species may be diurnal or nocturnal on the breeding grounds, with most small species being nocturnal; or a species may nest in the open or in cavities, with most small species being cavity nesters (e.g., Lack 1968). Defense against larid kleptoparasites likely also influences the dense coloniality of seabirds, attaining its extreme in the murre (e.g., Wittenberger and Hunt 1985, Burger and Gochfeld 1990). Spear (1993) has shown how annual variation in nesting density, among other things, in murre and cormorants can allow greater kleptoparasitism by gulls. Buckley and Buckley (1984) and others for eastern North America, and Mathiasson (1980), Parslow (1967) and others for Europe, chronicle the depressing effect that large populations of large-bodied gulls have on smaller larids, terns, and puffins.

Paine *et al.* (1990) have shown the potential direct and indirect effects of avian predators on the relative species composition of a breeding seabird community. On Tatoosh Island, Washington, as peregrine falcon populations recovered (from decimation owing to DDT pollution), those authors surmised that predation by the falcons led to decreased numbers of Cassin's auklets and rhinoceros auklets, two important prey species of the falcon. Thus, the auklet populations may have been artificially high for a few decades owing to the absence of an important predator. However, another important prey of the peregrine is the northwestern crow. The resurgent falcons reduced the crow populations as well, and this contributed to increased numbers of black oystercatchers, murre, and cormorants, which were parasitized by the crows. In this case, the size of the oystercatcher, murre, and cormorant populations may have been artificially low owing to the short-term absence of a biological control—predation by falcons—on kleptoparasitic crows.

Control of avian predators was a necessity in restoring tern and puffin populations in the Gulf of Maine (summarized in Buckley and Buckley 1984). Gull predation and kleptoparasitism was an important factor that limited the occurrence of tern and puffin breeding colonies. Well documented was the fact that the populations of common, roseate, and Arctic terns had decreased in New England during this century as the populations of gulls had increased. As the gulls were removed from islands (on the order of 10,000 birds) through poisoning and other means, the terns and puffins returned, aided by social attractants (Kress 1982, 1983; see Chapter 9e).

Changes in Climate

It has been claimed repeatedly that seabirds occur where their prey species are (e.g., Ashmole 1971), and as reviewed above, changes in prey composition can lead to regional changes in seabird distribution and numbers. In most cases, however, the situation may be more complex. In spite of decreased availability of nesting habitat (coastal wetlands) and increased disturbance from humans, colonies of elegant and royal terns, as well as of black skimmers, have been founded and numbers have increased in southern California during recent years. The recent invasion of royal terns, in fact, represents a return to their status of several decades previously (cf. Grinnell and Miller 1944, Ainley and Hunt 1990). The black skimmers have continued to spread northward and now nest in San Francisco Bay for the first time in recorded history (S. Terrill, pers. com.). Interestingly, black skimmers on the eastern coast of North America also have been invading (re-establishing) northward (Buckley and Buckley 1984).

Coincident with these northward shifts of southern species in California, the distributions of northern species have been retreating northward. Tufted puffins and common murrelets no longer breed in the southern California Channel Islands (one or two pairs at best for the puffin), although they did so in appreciable numbers near the turn of the century (cf. Hunt *et al.* 1980, Carter *et al.* 1992). Human-caused factors (e.g., oil spills) may have exterminated the colonies, but these colonies might have been remnants of previously larger colonies, as the old breeding sites have not been recolonized even after control of the degrading influence. During the past few decades, the ocean off California has been warming (Roemmich and McGowan 1995), and this factor may be involved in the faunal shifts in California. Of course, such a process has been played out on geologic time scales as well (e.g., Warheit 1992).

In Antarctica, as the environment has warmed and pack-ice cover has diminished in the past few decades, faunal shifts have occurred. In the Antarctic Peninsula, populations of chinstrap penguins and blue-eyed shags and, perhaps, brown skuas (along with sub-Antarctic elephant seals) have been increasing and colonizing areas southward; southerly species have been retreating (Ainley and Sanders 1989, Fraser *et al.* 1992, Ainley *et al.* 1995a). On the other hand, in the most southerly reaches of Antarctic seas (e.g., the Ross Sea), populations of the southerly breeding Adélie penguin have been increasing and spreading southward (Taylor and Wilson 1990), conceivably as diminishing pack-ice cover has provided greater access to food resources.

Ultimately, climate change also alters the availability of food in a region (e.g., Roemmich and McGowan 1995). Where this factor is involved, it is not so much a faunal shift that results, but rather a depression or enhancement of seabird population growth. Ainley and Lewis (1974) noted decadal changes in Cassin's auklet population size on the Farallon Islands, 1880s to 1970s, in response to climate-related changes in food availability—a pattern that is recurring in recent times (Ainley *et al.* 1994, Hill 1995). Aebischer *et al.* (1990) noted decadal changes in the environment, food, and seabirds in the North Atlantic, and Veit *et al.* (1997) have noted even more closely coupled changes in these factors in the California Current.

The decadal changes noted by Roemmich and McGowan (1995) are part of a shift in climate that has occurred since the mid-1970s and has produced changes in marine communities and seabird numbers throughout the north Pacific region, from north Pacific central waters (Venrick *et al.*

1987, Polovina *et al.* 1994) to the California Current (Ainley *et al.* 1995b, Veit *et al.* 1997), Gulf of Alaska, and Bering Sea (Springer 1992, Hollowed and Wooster 1995). All levels of the marine ecosystem have been affected. The importance of this shift is that restoration of seabird populations to levels attained before the mid-1970s is not possible under existing conditions.

IMPLICATIONS FOR THE RESTORATION OF SEABIRD POPULATIONS

In defining restoration or choosing restoration goals, when applied to seabirds (see Chapters 6, 10), it is important to consider whether or not the species' capacity to increase or at least maintain its numbers is a viable one. Then, if and when natural environmental factors cycle back to an earlier condition, population growth of the seabird population is likely. *Therefore, what needs to be restored as a minimum is the capacity of a population to respond to improved trophic and other environmental conditions* (see Chapter 6 for discussion of restoration goals). In that sense, then, the brown pelican, currently on the U.S. Endangered Species List, could be considered restored, as the population is no longer severely depressed and breeding success again fluctuates with natural fluctuations in food availability (Ainley and Hunt 1990).

Most important, as this review has revealed, food availability (and ultimately climate change) is the dominant factor in affecting long-term growth of depleted seabird populations. Managing for food availability, however, is a very difficult, problematic, and highly political alternative because the only practical way to do so is to curtail commercial fisheries. To date, only if seabirds on the Endangered Species List are at risk has attention been given to management of marine living resources to protect the endangered species (e.g., the anchovy management plans *vis à vis* brown pelicans; U.S. Department of Commerce 1978).

Much easier and better demonstrated is the option of managing predators and kleptoparasitic species to encourage recovery of seabird populations (e.g., Kress 1982, 1983). Breeding habitat can be restored (e.g., for albatross on Midway Island; Rice and Kenyon 1962), and disturbance to breeding islands can be controlled. These management tools require just the decision to implement them, with relatively minor political or social issues to consider.

Restoration of seabird populations to levels attained earlier this century, at least in the north Pacific, is likely impossible under present conditions. Climate change and dramatic changes in prey resources now negate such a goal. In isolated cases, even restoration of individual populations may not be attainable because of climate change (and effects on prey availability) after the population was decimated (e.g., restoring brown pelican breeding colonies to Monterey, California, or restoring common murre breeding colonies to the California Channel Islands). Each restoration project has to be evaluated with this possibility in mind.